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MIGRATION AS A FACTOR IN EVOLUTION: ITS ECOLOGICAL DYNAMICS, II.

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III. THE MIGRATIONAL FACTORS IN EVOLUTION

1. Introduction

From the preceding discussion of the principles of animal activity which underlie their behavior, attention is now directed in greater detail to suggestions for their application to migration. Emphasis is placed upon those relations which show the main causes of stress, the cycles of circulation caused by diversity, and the interaction, equilibrium, and adjustment operating between the various systems. I have not attempted to go into detail on the quantitative relations, although there is much physical and some ecological data, already organized, which illustrate the method of application. There is, however, but little quantitative distributional data which are at present available. The elaboration of this phase is urgently needed. Limiting factors retard and prevent the migration and diffusion of animals; these are the "barriers" so frequently mentioned by students of geographical distribution. As previously mentioned, two major systems or agencies are involved in this process, the animal and the environment. The locomotor activity of the animal is a phase of its general responses. The migrations of most animals are therefore not different, in any important features, from the ordinary daily life of the animals; that is, migrations are incidental and included within the ordinary responses. Anticipating somewhat, and speaking broadly, if animal responses are of evolutionary value

so must be the migratory ones. In detail there are innumerable animal peculiarities which influence migration, depending on the stage of development of the animal, its physiological and ecological conditions and characteristics, and the status of its environment. The large number of factors involved in this is no doubt an important conservative influence and checks the speed of interaction.

The word migration is used in several senses, so that for our purpose it is now necessary to define this more definitely. By migration is here meant the movement of animals from one place to another, and this includes, not only the causes and conditions of their migration, but their methods as well and the immediate result upon the animal. If all migrating animals perished at the end of their journey the study of its influence would be relatively simple.

In deference to those who are mainly interested in the animal and who are less interested in the environment it has been customary in many zoological writings to discuss animals first, and their environment later. But as zoology progresses and as explanations are resolved more and more into the sciences upon which it rests, greater and greater prominence is given to the physical causes and conditions of the environment. Viewed broadly, zoology should be made to fit into the general world system in such a manner as will best aid in understanding it, irrespective of our traditional habits of mind. For this reason this phase of the discussion will begin with the environment, as a factor in *passive migration or transportation*, and will lead up to the animal as a factor in its own migrations.

In the orientation of the major features of the world Powell recognized: the atmosphere, the hydrosphere, the lithosphere and the biosphere. These self-explanatory, relatively homogeneous, physically and mechanically distinct, and interacting systems, furnish the medium in which animals live and perform their migrations. We

may look upon these three physical systems as a result of existing temperature conditions of the earth. Increase the temperature to a certain amount and the atmosphere would be rarefied, the hydrosphere would disappear into the atmosphere as water vapor, and the solid earth would become fluid. Or, reverse the process, beginning with its present state, and should the earth cool progressively, the hydrosphere would become frozen to the solid phase and atmosphere would likewise be transformed to the solid state, and all these systems would become one. The present resolved and differentiated state is thus dependent on the present temperature conditions. The relation of equilibria between these three systems is one of the major problems for the application of the phase rule, and their methods of interaction is an unlimited field for the application of Bancroft's law, and both of these are of the greatest importance to all concerned with the gross environments of organisms.

In view of the dominating influence of temperature, we must not overlook the fact that temperature is only one of the essential conditions of life. It is important to observe that the present stratum of the earth's surface where organisms live is a remarkably narrow one, and only moderate departure above or below the condition in this stratum at once becomes limiting factors to organic activity. Chamberlin ('06, pp. 1-2) states this impressively as follows:

The narrowness of the range to which temperatures must be confined to permit progressive organic and intellectual evolution takes on its true meaning only when we recall that the natural temperature range on the earth's surface is sixteen times as great as this, while that affecting the solar family is at least sixty times as great. For a hundred million years, more or less, this narrow range of temperature has been maintained quite without break of continuity, unless geologists and biologists are altogether in error in their inductions.

The maintenance of such a dynamic system of equilibrium of the environment and of the organism, and the inertia of their systems—the tendency to continue or per-

sist in a given state—may well cause wonder and stimulate thought.

In the following analysis of the larger units which influence migration, those agencies will be used which serve as the basis for the smaller systems of action, and some of their main cycles of activity and methods of interaction will be indicated briefly.

2. Atmospheric Agencies in Transportation

The instability of the air, its numerous cycles of activity or circulation, hourly, daily, seasonally, annually, and those of longer duration, furnish an agency which has transported animals from one locality to another for ages. Gentle breezes carry small animals, while violent tornadoes carry larger ones. Small eggs, desiccated rotifers, entomostraca, and other small aquatic animals, have been transported long distances by the wind, and have thus found many favorable habitats, otherwise not available to them. The wind, reinforced by streams, even temporary ones, has transported animals long distances, as have the waves of the sea and inland waters. The winds, supplementing the flight of animals, have carried them thousands of miles beyond their normal range, as in the case of birds and insects. A vast literature has grown up recording the details of these findings, and yet about the only evolutionary conclusion which can be safely drawn from the multitude of facts is that by these processes animals have tried out and acclimated themselves to a vast number of isolated habitats which have tended to give them a varied and widespread range, and to that degree it has aided in their perpetuation.

The most definite evidence of atmospheric influence in evolution is perhaps the direct influence of climate and of climatic changes. Fortunately, for our present purpose, and mainly through the researches of Chamberlin (1897–1901) and Huntington ('15, pp. vi–vii), secular climatic cycles have been investigated. Chamberlin has related these intimately to the changes in the hydrosphere

and lithosphere, and he has indicated their modes of interaction in a strictly dynamic manner. He shows that during a period of land elevation and mountain formation, with cold, dry, diverse climatic differences and zonal arrangements on land and with a deepening of the sea, these conditions tend to change progressively toward a moist, warm, uniform and tropical condition, which is related to the land equilibrium developed during base-level on land, and a marine condition of extensive shallow seas. The process of adjustment to these strains beautifully illustrates Bancroft's law. It is not an accident that mountains are centers of origin and dispersal of animals, nor are they solely refuges where endemic forms escape the competition of the lowlands. Mountain regions in their elevation subject whole populations to severe climatic and other stresses of many kinds, depending on the physical and vegetational diversity of the region, and doubtless thus many animals become extinct, while others as individuals or as a race become acclimated to the new and changed conditions and thus survive.

It seems strange that, although dynamic principles are shown in almost ideal form in the unstable air, yet, as a whole, this phase of science seems to be somewhat backward in the formulation of the ideas of processes, so that their greater successful application is seen in geology. It appears that the reciprocal dynamic relations which exist between barometric lows and highs (both temporary and permanent) makes them dynamic centers of action (Fassig, '99) in a cycle of circulation and adjustment to stress. This idea is one which may profitably be extended to the interpretation of successive phases in the establishment of climatic dominance. The change from the Ice Age to that of the present, and the accompanying change of storm tracks (Adams, '09, pp. 45-46) are comparable to the seasonal change from winter to summer dominance, while passing through the transitional March weather stage. Furthermore, the summer and winter dominance are dynamic equilibria established by a balancing among

the various highs and lows (Adams, '15*a*, pp. 69-71). These transitional periods illustrate Bancroft's law in the process of establishing new relative equilibria. The dynamic centers are to be looked upon as concentrating, transforming and radiating centers, whose recognition and cycles of activity are an essential part in the application of Bancroft's law to the development of atmospheric equilibria.

3. Hydrospheric Agencies in Transportation

The waters of the earth are more dense than the air but are yet quite mobile, and undergo relatively rapid cycles of circulation, both in the sea and in inland waters.

(*a*) *Marine*.—The great currents of the sea, the tides, and the wind-formed waves, are very active agents in the transportation of animals. Not only are marine animals extensively transported, but also, in the long run, large numbers of land kinds, as the animals on oceanic islands testify, as shown by Wallace. And just as the processes of erosion operate upon land, and tend to reduce such areas to sea level, so the sea itself possesses its own cycles of transformation of its bottom and shores, tending to flatten them out to the equilibrium of the deep sea floor, transporting materials and redistributing them in response to its stresses, eroding here, depositing there, and always making changes in the conditions which not only transport animals, but as well, by the migration of the physical conditions, lead animals from one locality to another. Land animals are largely influenced by the surface conditions, while the marine ones are largely by sub-surface conditions.

(*b*) *Inland Water Bodies*.—Bodies of inland standing water, in their broad features, are smaller editions of the seas, as far as their waves, circulation and transporting powers are concerned. Their chemical character, whether fresh or saline, has more influence upon animals than the mechanics or their methods of circulation. The most marked influence of the inland waters is their rela-

tively small area, isolation, even though they may overflow into streams. Inland waters are in general relatively ephemeral in character compared with marine waters, because with progressive erosion of the land they tend to become extinct through deposition and ultimate drainage.

(c) *Running Waters*.—The transporting power of running water is easily evident. The constant direction of flow, its duration (as some drainage lines are of extreme antiquity), and repeated transportation, have subjected animals again and again to new conditions, and carried them to new localities. Streams transport both land and aquatic animals and by their persistence, activity, and the thoroughgoing fashion in which they work over the land surface, are one of the most powerful agencies of transportation. Streams undergo changes depending on the dynamic status of the stream. The greater stress to which the stream is subjected by uplift, the greater its velocity and its relative transporting power, and the nearer it erodes to base-level, the less current and relative transporting power it possesses. Most animals counteract the transporting power of the stream by definite responses to the current, and thus maintain their position and are not carried away.

4. *Lithospheric Agencies in Transportation*

The lithosphere includes the solid earth, which to the ordinary mind is the ideal of stability. The transporting power of the solid is, however, usually at a very slow rate, but this is not always the case, because of the suddenness of fracture. The solid ice of the glacier moves slowly and yet travels long distances, but usually does not transport an abundance of animals. Avalanches move with greater speed, but they operate in rather limited areas. Landslides transport, slowly or rapidly, large masses of land containing animals. All of these processes are dominated by gravity, and tend to transport animals from a higher to a lower altitude. Perhaps

the most powerful motion of the solid earth is seen in the crustal movements, associated with the cycle of isostasy, which elevates and depresses the surface of the land in relation to sea level. In this is seen an essential condition which has made all land life possible, because without such movements all the land would have been washed into the larger dominating sea. The great land elevations, such as those which produce plateaus and mountains, have transported whole faunas, covering thousands of square miles, upward, and have subjected them to great stress, through long periods of time. Such elevations as arise in a region unfavorable to animals, may improve them, as in the case of high mountains, rising on a dry desert, but often such elevations, which are departures from the favorable thin surface stratum, are in the direction of unfavorable conditions and of limiting factors. Broadly speaking, depressions below sea level are similarly limiting to marine organisms, and these have operated on a magnificent scale. The mountain tops, like the deeps of the sea, are relatively animal deserts, both are extreme departures from the conditions which are normal to most animals.

The most rapid physical agency in the transportation of animals on land is the influence of running water and that of the wind. These forces operate in short cycles and intensively, in contrast with the movements of the solid earth.

Volcanic activity has probably been only a minor factor in the transportation of animals, although in a secondary way, in conjunction with other agencies, as currents of water, porous materials buoyed by air, may act as a raft in their transportation. But indirectly by building mountains, islands, etc., it has had an influence similar to that of the crustal movements of the earth in forming new habitats, and has thus had a powerful effect.

5. *Biospheric Agencies in Transportation and Migration*

(a) *Plants*.—The relatively sedentary and rooted condition of plants caused Cope to aptly call them “earth parasites.” With this stable habit and the unstable environment, rooted plants have been forced to develop a line of fracture, as it were, between themselves and the environment, which has permitted them, by their exceptional powers of dispersal, to spread rather freely at some stage, and to thus scatter over much of the available surface of the earth. As far as the actual movements of plants are concerned, unaided by winds, waters, and animals, but solely by growth and similar movements, plants have probably had but relatively small influence upon animal transportation, although secondarily, by the spreading of vegetation and the changed conditions which this causes, they have permitted extensive transportation and migration of animals. The specific gravity of wood, its buoyancy in water, and the various sails, vanes, and structures which favor wind dispersal, and all the hooks and claws which help make various kinds of burrs, and the edible fruits which animals devour, all combine to favor transportation by wind, water, animals, and other active agencies. By these means, animals living within, or on such transported parts, may be buoyed and transported by waves, currents of water or air, and be carried by animals for long distances, and into new localities and conditions.

(b) *Animal Migration*.—The movements of animals which take them from one locality to another are exceedingly diverse. They vary not only with the character of the animal, at different stages in its life history both structurally and functionally, and also under varied environmental conditions. The fixed and sessile animals more nearly approach the conditions found commonly among plants, but among animals this habit is confined mainly to aquatic animals, that is, to animals living in a mobile medium, which transports them at some stage.

The most important character which influences the migration of animals is its own powers of movement. These movements are dependent upon the ecology and the physiology of the animal, its structure and its mode of response. The general principles of response have been discussed in the first part of this paper, where the systems of activity, the cycles of activity, the limits of activity, and the interaction of all systems was emphasized. All of these factors should now be recalled. Animals creep, walk, swim, and fly, according to the media in which they live, their structure, and their ecology, and the interaction of all these factors put limitations upon animal movements.

From the standpoint of function, animal movements and migrations have two main influences. By movement the animal subjects itself to new conditions, these conditions have a direct influence upon the animal, and change the direction or its internal changes, and it becomes acclimated or dies; or by its repeated responses and retreating movements, it escapes from the adverse conditions and finally comes to rest in a new relatively favorable condition (Adams, '15, p. 12). This monotonous cycle is repeated with all the variations which diversity of animals and diversity of conditions can produce, and in its essential features it is the same from Protozoa to man.

The geological age in which we live is one in which the land surface, relative to the sea, has accumulated uplift from former ages, and has been newly elevated, and as a result there are many high mountains, and the seas are relatively deep. These are conditions of stress, and the processes of adjustment to strain are in full operation. This is a period of relative diversity of the lands and of the seas, which favors diversity, both in the atmosphere and in the hydrosphere. With the elevation of the land, this diversity is shown both vertically and horizontally. Large areas lie at considerable altitudes and in their departure from the narrow mean surface

stratum, are subjecting many animals to stress, and to the process of acclimatization to the high altitude conditions. The climatic diversity shown vertically, also expresses itself longitudinally, by interference with free circulation of temperature, moisture, and other climatic factors, and tends to produce the varied climatic zones, such as tropical, temperate, and polar, as well as the diversity due to humidity. These diversities mean that many minor circulating systems are caused and consequently there are varied local wind systems, further favoring diversity. All of these influences tend to favor local or relatively limited migration, rather than the widespread dispersal of animals subjected to such conditions.

The hydrosphere is influenced similarly. The diversity of the lands favors diversity in inland waters, and the arid climates favor saline waters. Inland waters under these conditions tend to be isolated and varied. In the sea the deepened waters produce stresses similar to those on land produced by altitude, and the elevations and relative increase in the land area interferes with the circulation of marine waters and favors local differences and local stresses. With the deepening of the seas, the shallow waters are restricted and the littoral animals are under increased stress. It is seen, therefore, that the conditions dominant on a world scale are those of stress or strain, now in the process of adjustment. It should be observed that all spheres, the atmosphere, hydrosphere, lithosphere, and the biosphere are involved in the same general interacting process. It is only by viewing the subject broadly that we thus gain this perspective of the status of our own times.

We may now turn to certain details which will help to illustrate the application of these ideas to animal migration. The same grouping of influences will be used which has been applied in the preceding discussion of passive migration.

(a) *Atmospheric Influences*.—The atmospheric factors

which influence active animal migrations are mainly those which are dependent upon: chemical composition (largely oxygen, CO_2 and volcanic gases); temperature; pressure; humidity; and mechanical effects, as they are combined in climatic changes. All of these influences undergo differences which influence, by acceleration or interference, the movements and migrations, acclimatization and ecological attunement of animals. Furthermore, these influences, or their systems, do not act independently but at the same time, so that their laws of interaction are the main rules of the game.

(b) *Hydrospheric Influence*.—The hydrospheric influences are similar to those of the air, depending on: composition (salts and gases); temperature; pressure; and mechanical effects (waves, tides, circulating currents). In this geological age of stress and diversity, on account of the mobility of this medium, it has transmitted its pressure with slight friction to animals. Upon land the active streams are a direct response to the steep slopes down which they flow, and they visualize at once the reality of this active media which has kept fishes and other animals busy moving up stream for millions of years. Bodies of standing water, by their isolation, except when connected with streams, tend to retard active animal migration. Such bodies are likely to abound in the early stages of uplift and to decline as drainage lines develop. The diversity of climate into humid and arid as previously mentioned, tends to favor diversity, chemically, in bodies of standing water. These inland waters, while discontinuous to many aquatic animals, are not so to many flying and running kinds.

In the sea, the narrowing of the continental shelf tends to crowd the shore animals, and favors isolation and diversity of habitat, and retards ready migration for many animals. The hastened erosion, however, tends to increase the continental shelf and its continuity. The deeper water shows relative diversity and tends toward stagnation in its currents because of the relative increase of the land area.

(c) *Lithospheric Influences*.—The interdependence of the physical spheres is so marked that by this time, in the discussion of the air and water, the solid earth has been included in part. The rigidity of the lithosphere is so great that its adjustments to strain are in general relatively slow and of long duration. The density of the medium is so great that animals inhabit only a shallow surface stratum, the upper part of the zone of weathering processes, in or on the soil. Animals living in the soil are influenced by its density, its physical and chemical composition, temperature, and its movements. Those living on it are relatively independent of the qualities just mentioned, but are much influenced by the relief of the surface, by the climate and vegetation, and are more truly air rather than earth dwellers. The elevation of the land above sea in itself, and not as modified by climate and topography, probably has little direct influence, except in its degree of stability with regard to erosion. The greater the altitude and the steeper the slope, the greater the physical stress and the rapidity of erosion. Ice and landslides exert pressure and drive animals before them, and are largely dependent on elevation and slope. The cycle of degradation of the land, particularly its topographic diversity, greatly influences the degree of freedom in the movement of land animals.

(d) *Plant Influences*.—The stresses of the physical environment in the air, water and earth, impose pressure upon the vegetation. Since the largest number of animals are directly dependent, and a smaller number indirectly upon plants, much of this pressure is transmitted to animals. The climatic diversity, seasonal and secular cycles, influence the amount of animal food. Some animals, during adverse seasonal conditions and scanty food supply pass into an inactive state, and tide over such a season, and most animals not possessing such tend to migrate. Thus upon the plains the bison wandered with the seasonal changes of pasture, just as mountain sheep and goats migrate up and down the slopes as their pasture

varies with the season. The succession of vegetation upon all surfaces, drives out some animals, just as it invites others to follow with it, as when, with the development of forest, the animals of the open find conditions unfavorable. The kind of vegetation, whether herbaceous, woody, conifer or deciduous, etc., has an important influence upon the movements of many animals. The cycles of vegetation also change the physical conditions, the temperature, humidity, soil conditions, and thus influence animals.

(e) *Animal Migrations*.—The individual migrations of animals, caused by their own spontaneity, and that by

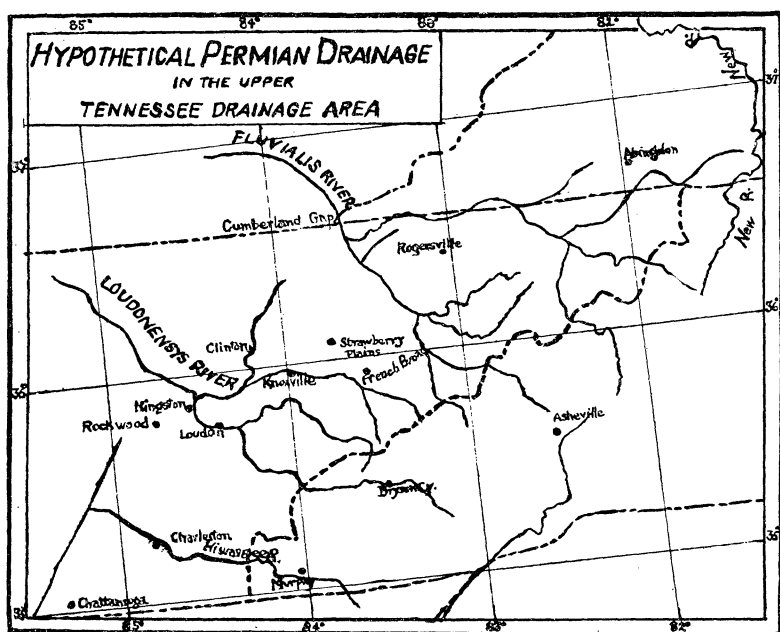


FIG. 1. Map showing the hypothetical Permian drainage of the Upper Tennessee drainage area. Compare with the present drainage shown in Fig. 2.

other animals, are exceedingly varied. All the factors which influence individual movements, as indicated in the first part of this paper, now apply in detail, and in addition there is the pressure exerted by animals living associated with them. Simple animals require a favorable

environment as truly as complex ones. It is known that many animals decline in vigor if kept in the same medium, but if the medium is kept fresh, or the animal moves about freely and secures a fresh medium, it thrives. Freedom of movement thus permits the animal to move away from influences which interfere with its system, and thus minimizes the disturbance. The continuation of this process tends, with freedom, to bring the animal ultimately into favorable non-interfering conditions if

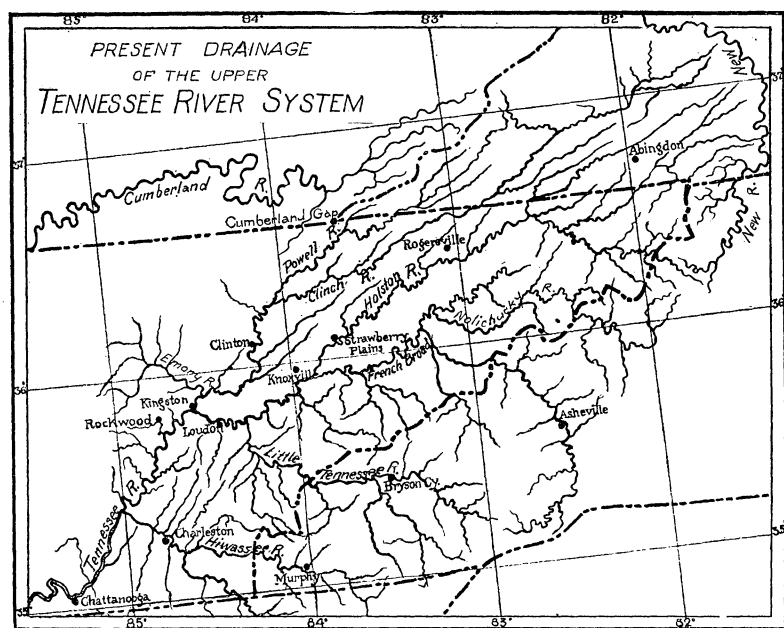


FIG. 2. The drainage of the upper Tennessee River system.

such exist. With these ideas in mind we need to recall that the atmospheric, hydrospheric, lithospheric and vegetational pressure all combine to encroach upon the animal, and to interfere or reinforce its activities and movements. The normal movements of the animal, and the ordinary routine of environmental changes, are thus in process of continual adjustment. Thus with the migration of the animal habitat, whether caused by a change in the atmosphere, hydrosphere, lithosphere, vegetation,

Fig. 4. The shells of these snails are shown in Fig. 5. The presence of these snails in the headwaters of streams appears to be due to the ordinary creeping movements of the snails taken in connection with the up-stream migration or growth of the stream habitat, because, on the other hand, the current tends only to favor a down-stream dispersal. Such animals, therefore, appear to be led about *by the migration of their habitat*. This sort of migration is comparable to those land migrations which

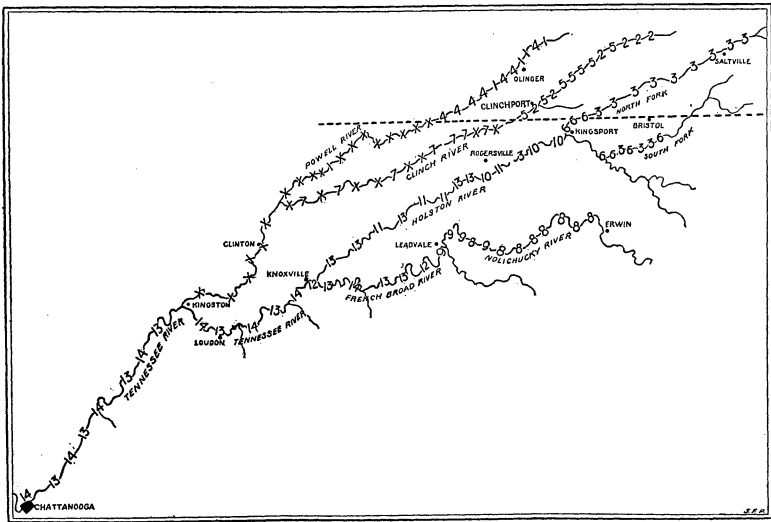


FIG. 4. Map showing the present distribution of the forms of the snail *Io* in the upper Tennessee River system. The numbers refer to the kind of shell illustrated in Fig. 5.

have clearly taken place during climatic migrations, as during the ice age, and during similar changes in humidity, and with base-leveling changes (Woodworth, '94; Adams, '01).

The competition among different kinds of animals has long been recognized as an important factor in animal migrations. Overcrowding produces a condition of stress, and as a result of this stimulus, animals tend to migrate and become diffused from the region of pressure in all possible directions. Thus new conditions are encountered which necessitate changes on the part of the animal, and thus this process continues indefinitely.

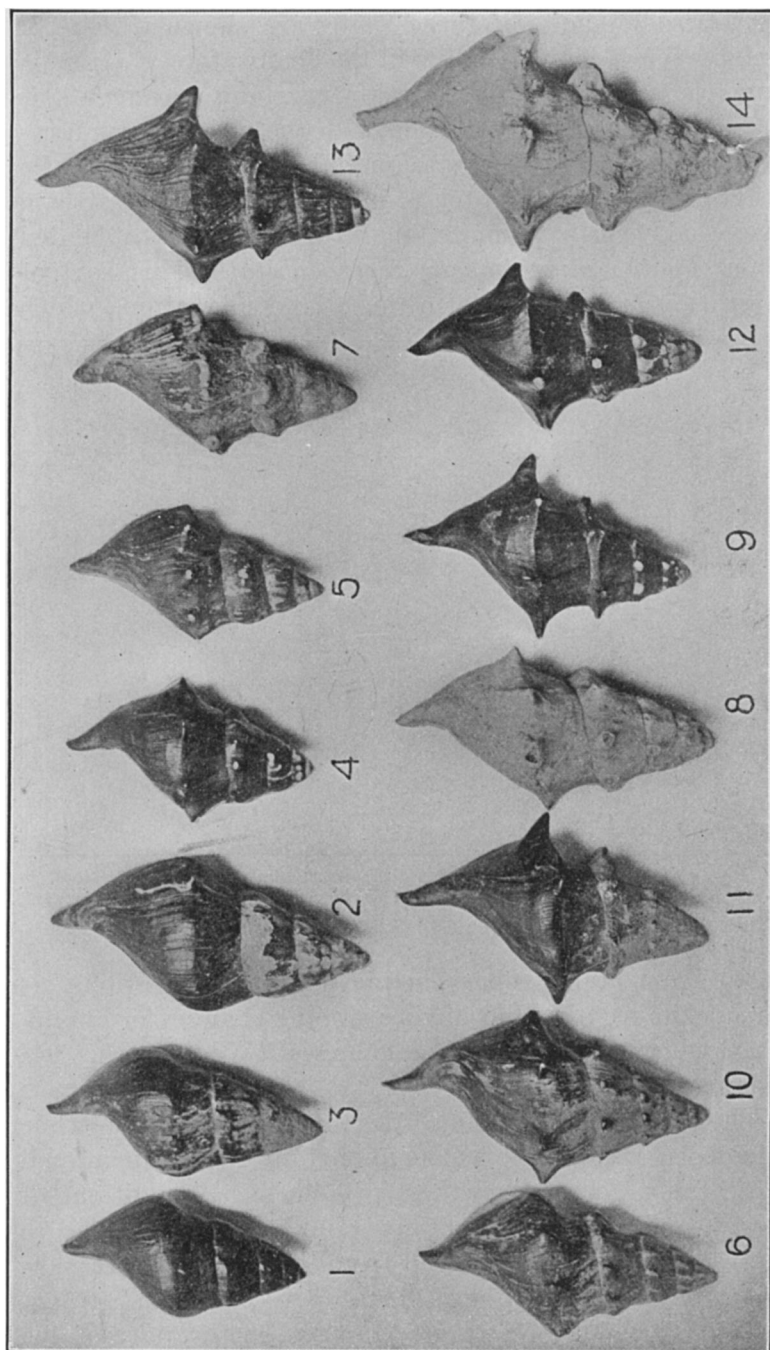


FIG. 5. Illustrations of the main forms of shells in the genus *Io*, whose hypothetical migrations are indicated in Fig. 3.

IV. SUMMARY AND CONCLUSIONS

The animal should be looked upon as a *dynamic system* which tends to continue in its course of action until changed from within or until diverted by external interference with its system, and until a condition of relative equilibrium is developed by balancing all influences. The behavior of animals should be viewed as a *process* of rhythmical activity.

The *cycle of activity* of the animal agent is a unit of fundamental importance. To study cycles, their *dynamic status*, their degree of relative equilibrium must be determined. In this manner the conditions of stress, the processes of adjustment to strain, and the conditions of relative equilibrium may be recognized and determined. These determinations should be applied to all cycles of activity, that of the life history, and all others. The use of these ideas enables one to apply Bancroft's law—that a system tends to change to minimize external disturbance—to animal activities, and thus one is enabled to explain a large number of diverse observations. Supplementary to Bancroft's law are the influences which tend to accelerate or reinforce, without other change, the condition of the animal.

The *activities of animals* cause them to collide with their environment. Conditions under which animals have become accustomed or attuned are those of relative equilibrium. With departure from these conditions, the animals are stimulated, their system is interfered with, and the animal tends to change until the interference is minimized. The hindrance thus placed upon animal activities are its "limiting factors," and these are to be viewed according to Bancroft's law. This law is not limited to the actions of the individual animal, but includes also the race, and those of animal associations. The Vernon-DeVries law of the *diminishing influence of the environment progressively during ontogeny*, is an example of limiting factors according to Bancroft's law. This law of Vernon's is of great value in the study of

migration in relation to evolution because it suggests the *critical period* at which the stress of the new environment may have its *greatest direct influence upon the new generation* and thus influence its heredity.

The next important category above the animal system is the *law of interacting systems*. The main models of interacting systems are:

1. The physical model of interacting forces, recalling in this connection the law of *inertia*, the tendency of a body to continue in its present state at rest, or in motion, and the law of reinforcement or acceleration.

2. Bancroft's law is that a system tends to change in such manner as to minimize external disturbance. This should be applied to the interaction of all systems. This is a law concerned with responses to stress and to the process of adjustment, and it shows development or evolution of *equilibria*.

3. The phase rule applies to the *result* of responding to stress or *equilibria*. This is thus complementary to Bancroft's law; one is concerned with the condition of stress, and the other with the condition of equilibria.

These laws appear to be universal and not limited solely to the non-living. Irritability may not be causally explained, but *it seems to obey these general laws in the same manner as causal changes*. Applying these laws to animal migration, we see that the present geological age is one of physical stress, and that the process of adjustment to strain is now in operation. The physical stress applies to the air, water, earth and to their interactions. This is an age of physical diversity—tending toward one of simplicity and uniformity. With diversity there are many local cycles of activity in all features of the environment. These cycles of circulation influence the *transportation* of animals, and their active *migrations*. By transportation and migration animals encounter new conditions, new stresses, and change to minimize the disturbance and acclimate themselves to the limit of their

possibilities; and they repeat this cycle with unending monotony and persistence.

December 15, 1917.

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Although these books by Spencer are in many ways not representative of the more recent conceptions, yet strange as it may seem to some, I have seen no better general discussion of biological problems which uses so many thoroughgoing dynamic conceptions. After familiarity with more modern views, these books may be read with great profit, particularly his discussions of cycles, relative equilibria, and his general conception of life processes. See footnote on page 488. Bancroft and Child make no reference to Spencer. Cf. Höffding, Darwin and Modern Science, 1910, pp. 450-455.

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ERRATA

- P. 471, line 23 from top, third word should read "the."
P. 472, line 5, for "ontology," read "ontogeny."
P. 482, line 29, for "really," read "readily."